

New fossil *Bathymodiolus* (sensu lato) (Bivalvia: Mytilidae) from Oligocene seep-carbonates in eastern Hokkaido, Japan, with remarks on the evolution of the genus

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ABSTRACT

A new species of the genus *Bathymodiolus* (sensu lato) is herein described from the lower Oligocene Nuibetsu Formation in eastern Hokkaido, Japan. This is the oldest species of this genus in Japan and the second oldest world wide. Based on occurrence and distribution of fossil *Bathymodiolus* (sensu lato), we suggest that the “genus” spread to the whole world by the late Miocene. This dispersal pattern is supported by molecular studies and similar to that of the large vesicomyids.

Additional keywords: Oligocene, fossil, biogeography, Mytiloidea

INTRODUCTION

Bathymodiolus (sensu lato) is one of the representative members of chemosynthetic communities frequently found at hydrothermal vents and cold seeps. Phylogenetic relationships between *Bathymodiolus* (sensu lato) and other modioline mussels are of considerable interest, since Distel et al. (2000) hypothesized that *Bathymodiolus* (sensu lato) in the seep and vent sites originated from small wood- or bone-associated modiolines. The recent description of *Vulcanidas* from a shallow vent site by Cosel and Marshall (2010) suggests that pathways of adaptation occurred at least three times in the bathymodiolines. It is necessary to examine such pathways of adaptation from the view point of the fossil record.

Six Recent species of this genus are known around Japan (Sasaki et al., 2005). Morphologically, the genus can be classified into the four groups *Bathymodiolus thermophilus*, *B. brevior*, *B. heckerae*, and *B. childressi* (see Cosel, 2002). Most molecular studies, however, indicate that the genus is not a monophyletic group but includes instead several distinct clusters (e.g., Miyazaki et al., 2004; Jones et al., 2006; Iwasaki et al., 2006; Samadi et al., 2007; Fujita et al., 2009). Based on these studies and their morphological data, Cosel and Janssen (2008) recognized the following three clades, the

B. thermophilus, *B. aduloide*s, and *B. childressi* clades. Moreover, the *B. childressi* clade was subdivided into six groups, including the genus *Gigantidas* Cosel and Marshall, 2003 as one group. Among them, the *B. thermophilus* clade includes *B. thermophilus*, *B. brevior*, *B. heckerae* groups of Cosel (2002). Recently, Miyazaki et al. (2010) examined COI and ND4 genes and divided *Bathymodiolus* into four groups that correspond to three clades of Cosel and Janssen (2008) and one clade of the genus *Tamu* Gustafson, Turner, Lutz, and Vrijenhoek, 1998. Very recently, Lorian et al. (in press) also suggested that Bathymodiolinae should be split into the *B. thermophilus* and *B. childressi* groups, based on the studies of COI mtDNA and 28S rRNA. As a conclusion, the genus *Bathymodiolus* is not a monophyletic group, but consists of two or three clades. Strictly speaking, the genus *Bathymodiolus* should be used only for the molecular clade including the type species, *B. thermophilus* Kenk and Wilson, 1985. However, some authors used *Bathymodiolus* (sensu lato) to the clades other than *B. thermophilus* clade (e.g., Cosel and Janssen, 2008; Kiel et al., 2010). In this paper, we use *Bathymodiolus* (sensu lato) for all species hitherto described as *Bathymodiolus*.

The fossil record of *Bathymodiolus* (sensu lato) can be traced back to *B. willapaensis*, which dates from the middle Eocene (Kiel, 2006). In Japan, only three certain and two doubtful fossil records of *Bathymodiolus* (sensu lato) are known from cold-seep sites. One of these records is from the middle Miocene Akanuda Limestone of the Bessho Formation in central Nagano Prefecture. Kuroda (1931) described *Tamarindiformis akanudaensis* as a new species from Akanuda, Matsumoto City. Then, Tanaka (1959) illustrated this species as *Volsella*. Recently, Nobuhara et al. (2008) mentioned that the species possibly belongs to the bathymodiolines, based on the morphology of its juvenile shell. This species has been also illustrated from a large seep carbonate of the uppermost middle Miocene Ogaya Formation in Niigata Prefecture (Amano et al., 2010). “*Bathymodiolus*” sp. has been obtained and illustrated from siltstone of the

Pliocene Tamari Formation in Shizuoka Prefecture by Nobuhara (2003). In addition to these records, Katto and Masuda (1978) illustrated one specimen from the carbonate of the Oligocene(?) Muro Group in Wakayama Prefecture as *Modiolus* sp. This species occurred in association with *Conchocele* cf. *nipponica* (Yabe and Nomura, 1925) and *Callista* cf. *hanzawai* (Nagao, 1928) (= probably not *Callista*, but a vesicomid). Moreover, Amano et al. (2004) found several specimens of *Bathymodiolus*? sp. in mudstone of the middle Miocene Higashibessho Formation in Toyama Prefecture.

Fortunately, we could collect many bathymodioline specimens of a new species from an Oligocene deposit in Urahoro-cho, eastern Hokkaido. This is the oldest record in Japan at the moment. In this paper, we describe it and discuss its biogeographic significance and evolutionary trend of *Bathymodiolus* (sensu lato).

MATERIALS

The new species described herein is from limestones of the lower Oligocene Nuibetsu Formation which crops out along the Atsunai River, 1.5 km east of Kami-Atsunai railway station in Urahoro-cho, eastern Hokkaido (Figure 1). The limestone can be subdivided into three parts from bottom to top; limestone yielding many fossils and mudstone breccias (10m thick), laminated limestone without fossils (2 m thick) and limestone yielding pebbles of slate, plant debris and fossils (4 m thick). Carbonate minerals of the lower limestone precipitated in an early diagenetic stage are depleted in ^{13}C ($\delta^{13}\text{C}$ values as low as -49‰ vs. PDB; Pee Dee Belemnite standard), which indicates methane seep activity (Peckmann and Thiel, 2004). Although both lower and

upper parts yield chemosynthetic bivalves, and carnivore or scavenging gastropods, *Bathymodiolus* (sensu lato) was collected only from the parts, in association with the thyasirid *Conchocele bisecta* (Conrad, 1849), the vesicomid *Hubertschenckia ezoensis* (Yokoyama, 1890), the solemyids *Acharax* aff. *gigas* (Kanno, 1960), *A.* sp., the naticid *Euspira meisensis* (Makiyama, 1926) and the buccinid *Colus* cf. *fujimotoi* Hirayama, 1955. Terminology of description follows Gustafson et al. (1998). All specimens are stored at the Joetsu University of Education (JUE).

SYSTEMATICS

Family Mytilidae

Genus *Bathymodiolus* Kenk and Wilson, 1985

Type Species: *Bathymodiolus thermophilus* Kenk and Wilson, 1985 from hydrothermal vent fields on the Galapagos Rift.

Bathymodiolus (sensu lato) *inouei* new species
(Figures 2–6, 9, 11, 12)

Diagnosis: A small-sized *Bathymodiolus* (sensu lato) with elongate shell, beak near anterior end, nearly straight dorsal and ventral margin; blunt ridge running from umbo to posterior corner.

Description: Shell of small size for genus, up to 45.4 mm long, modioliform, elongate (height/length ratio = 0.30–0.59; length/height ratio = 1.71–3.31), equivalve and inequilateral, moderately inflated, sculptured by growth lines only. Blunt ridge running from beak to posteroventral corner. Beak prosogyrate, situated near anterior end (position of umbo; 2.3–6.9 % of shell length from anterior end). Anterior margin broadly

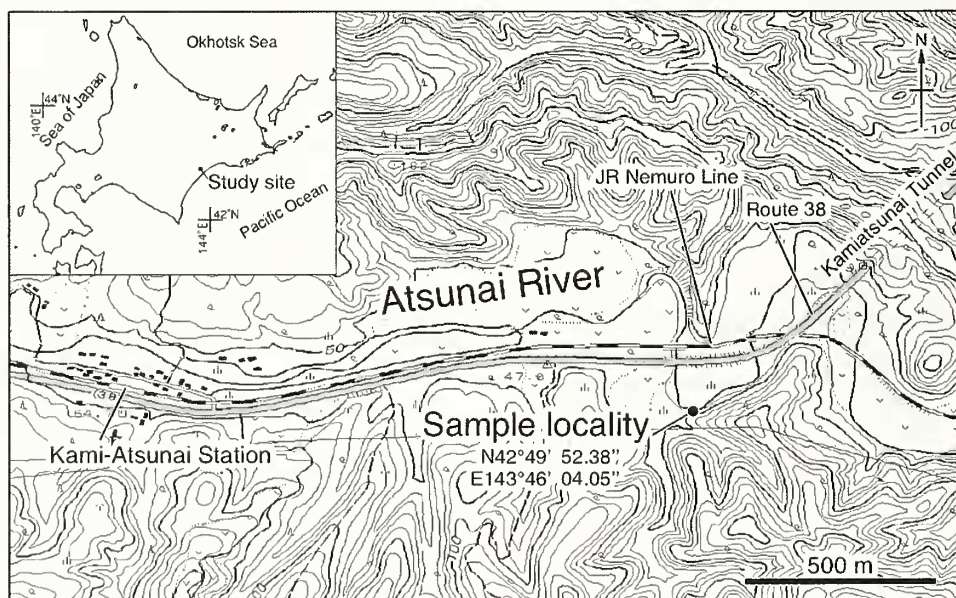
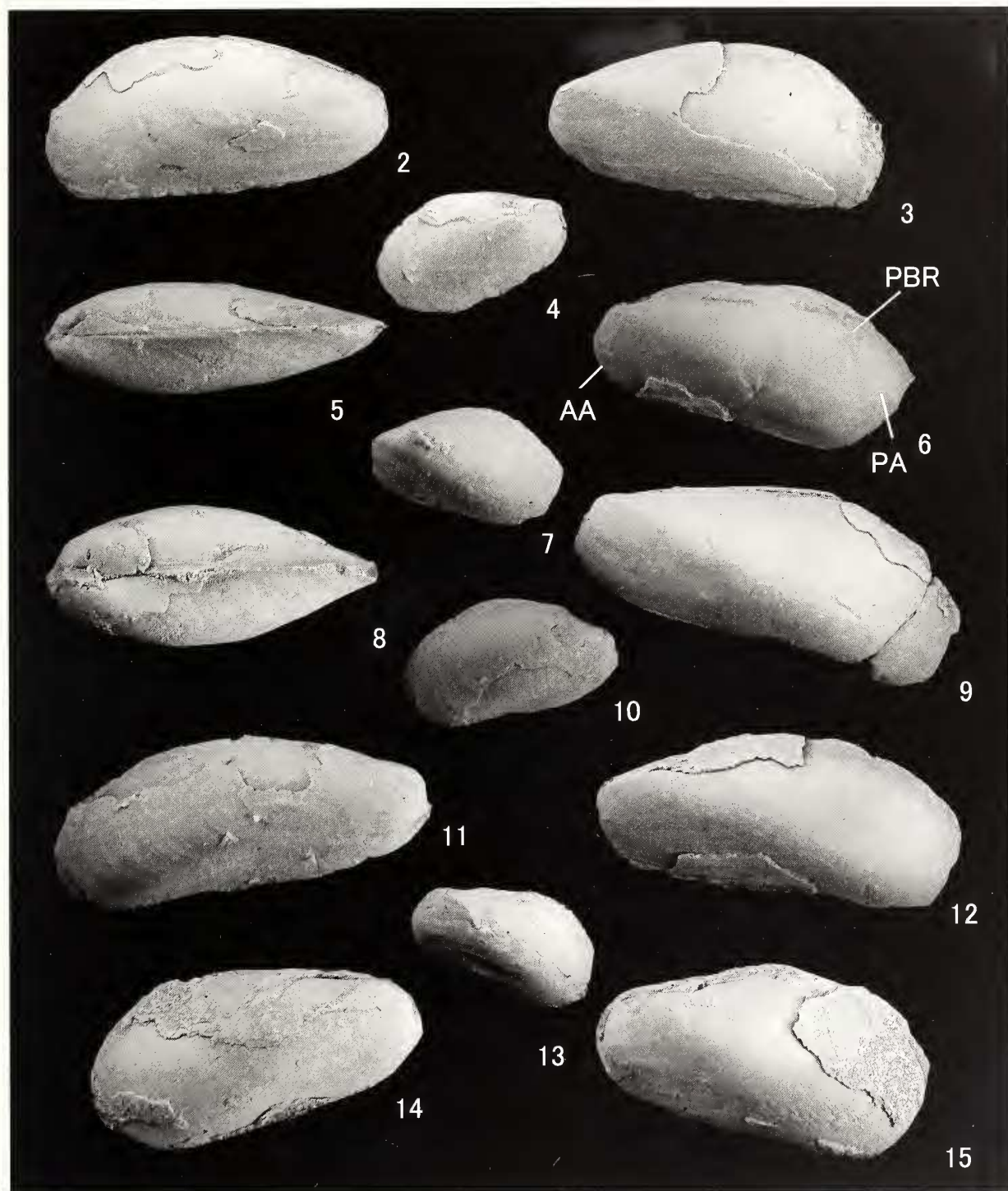


Figure 1. Locality map.



Figures 2–6, 9, 11, 12. *Bathymodiolus* (sensu lato) *inouei* new species. All specimens from type locality. **2, 3, 5.** Holotype, length 28.7 mm, JUE no. 15873. **2.** Right valve. **3.** Left valve. **5.** Dorsal view. **4.** Paratype, length 8.7 mm, JUE no. 15874-5, right valve (juvenile). **6.** Paratype, length 28.4 mm, JUE no. 15874-4, left valve; AA, anterior adductor scar; PA, posterior adductor scar; PBR, posterior byssal retractor scar. **9.** Paratype, length 30.5 mm, JUE no. 15874-3, left valve. **11.** Paratype, length 30.8 mm, JUE no. 15874-1, right valve. **12.** Paratype, length 31.1 mm, JUE no. 15874-2, left valve. **Figures 7, 10.** *Bathymodiolus* (sensu lato) *willapaensis* (Squires and Goedert). Topotype from Bear River deposit, Washington State, USA, collected by RJ. **7.** Length 11.8 mm, JUE no. 15876-1, left valve. **10.** Length 13.8 mm, JUE no. 15876-2, right valve. **Figures 8, 13–15.** *Bathymodiolus* (sensu lato) *akanudaensis* (Kuroda). **8, 14, 15.** Topotype specimens. **8.** Length 29.6 mm, JUE no. 15882-1, dorsal view; **14.** Length 22.4 mm, JUE no. 15882-3, right valve. **15.** Length 24.2 mm, JUE no. 15882-2, left valve. **13.** Length 15.4 mm, JUE no. 15883, left valve, loc. Kita-Kuroiwa, Joetsu City.

arched; ventral margin nearly straight; posterodorsal margin very broadly arched, continuing into steeply sloping posterior margin. Hinge edentulous. Nymph extending from beak and occupying 55% of dorsal margin. Anterior adductor muscle scar distinct, small and semicircular; posterior adductor scar large and ovate; posterior byssal retractor scar long, thin, united with posterior adductor scar.

Holotype: JUE no. 15873.

Paratypes: JUE no. 15874-1 to JUE no. 15874-5; all from the type locality.

Type Locality: Outcrop along the Atsunai River, 1.5km east of Kami-Atsunai Railway Station in Urahoro-cho, eastern Hokkaido.

Material Examined: Eighty specimens were examined. Among these, forty-six are articulated.

Measurements: See Table 1.

Remarks: The new species can be identified as *Bathymodiolus* (sensu lato) because of its modioliform shape and the occurrence from the cold seep site. Owing

to its terminal umbo and its continuous posterior retractor scar united posterior muscle scar, the new species may be assigned to the *B. childressi* clade by Cosel and Janssen (2008).

Comparison: The Eocene species *Bathymodiolus willapaensis* (Squires and Goedert, 1991) (Figures 7, 10) has very similar outline to juvenile form of the present species, but has much smaller (27 mm long) and higher shell than *B. (sensu lato) inouei* new species (figure 16). Also, *B. akanudaensis* (Kuroda, 1931) from the Miocene Bessho and Ogaya Formations (Figures 13–15) can be discriminated by having distinctly higher and more inflated shell than the new species (Figures 16, 17). *Bathymodiolus* (sensu lato) *inouei* resembles *Bathymodiolus* (sensu lato) *palmarensis* Kiel, Campbell and Gailard, 2010, from the “Oligocene” deposit of Colombia, in its elongated shell and its beak located near anterior end, but differs from it by having less distinct ridge and less expanded posterior part. *Volsella yokoyamai* Hatai and Nisiyama, 1952 described from the upper Eocene Iwaki Formation in Fukushima Prefecture resembles *B. (sensu lato) inouei* in having an elongate shell, but differs by its well inflated shell, more posteriorly located beak and more distinct ridge. One specimen illustrated by

Table 1. Measurements of *Bathymodiolus* (sensu lato) *inouei* new species.

Specimens	Type	Length (mm)	Height (mm)	H/L	L/H	Anterior length (mm)	Position of umbo (%)	Width (mm)
JUE no. 15873	Holotype	28.7	13.3	0.46	2.16	1.6	5.6	9.1
JUE no. 15874-1	Paratype	30.8	12.0	0.39	2.57	1.4	4.5	10.1
JUE no. 15874-2	Paratype	31.1	13.4	0.43	2.32	0.7	2.3	9.8
JUE no. 15874-3	Paratype	30.5	12.3	0.40	2.48	2.1	6.9	8.7
JUE no. 15874-4	Paratype	28.4	14.4	0.51	1.97	1.5	5.3	9.7
JUE no. 15874-5	Paratype	8.7	5.1	0.59	1.71	0.5	5.7	3.0
JUE no. 15875-1	Topotype	45.4	13.7	0.30	3.31	-	-	-
JUE no. 15875-2	Topotype	29.1	13.6	0.47	2.14	0.8	2.7	9.3
JUE no. 15875-3	Topotype	30.2	12.4	0.41	2.44	0.7	2.3	-
JUE no. 15875-4	Topotype	27.7	12.4	0.45	2.23	1.5	5.4	8.6
JUE no. 15875-5	Topotype	24.2	12.3	0.51	1.97	1.1	4.5	6.6
JUE no. 15875-6	Topotype	25.0	11.6	0.46	2.16	1.3	5.2	-
JUE no. 15875-7	Topotype	24.7	10.7	0.43	2.31	1.3	5.3	-
JUE no. 15875-8	Topotype	27.1	12.2	0.45	2.22	1.3	4.8	8.8
JUE no. 15875-9	Topotype	27.0	12.9	0.48	2.09	1.2	4.4	9.3
JUE no. 15875-10	Topotype	23.4	10.5	0.45	2.23	1.1	4.7	-
JUE no. 15875-11	Topotype	21.2	9.7	0.46	2.19	1.0	4.7	-
JUE no. 15875-12	Topotype	20.4	10.0	0.49	2.04	1.4	6.9	6.5
JUE no. 15875-13	Topotype	19.8	9.2	0.46	2.15	0.8	4.0	6.7
JUE no. 15875-14	Topotype	18.8	10.2	0.54	1.84	1.2	6.4	6.7
JUE no. 15875-15	Topotype	19.2	9.1	0.47	2.11	-	-	6.1
JUE no. 15875-16	Topotype	17.8	8.0	0.45	2.22	1.1	6.2	5.2
JUE no. 15875-17	Topotype	16.3	9.1	0.56	1.79	0.7	4.3	4.9
JUE no. 15875-18	Topotype	13.8	6.7	0.49	2.06	0.7	5.1	4.3

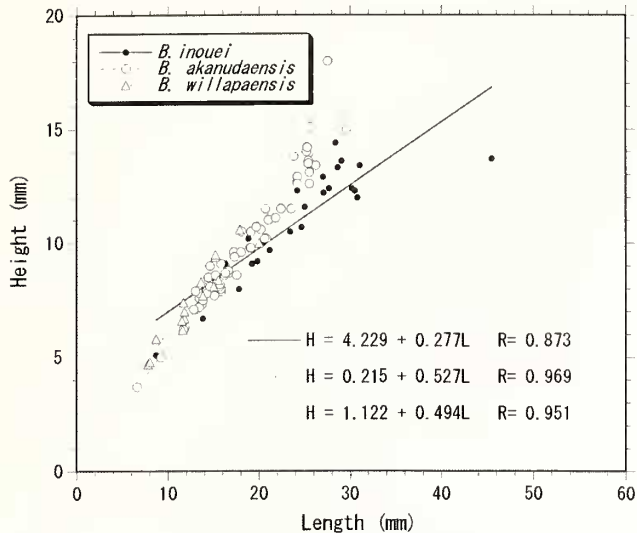


Figure 16. Ontogenetic changes in shell length and height of *Bathymodiolus* (sensu lato) *inouei*, *B.* (sensu lato) *willapaensis* and *B.* (sensu lato) *akanudaensis*.

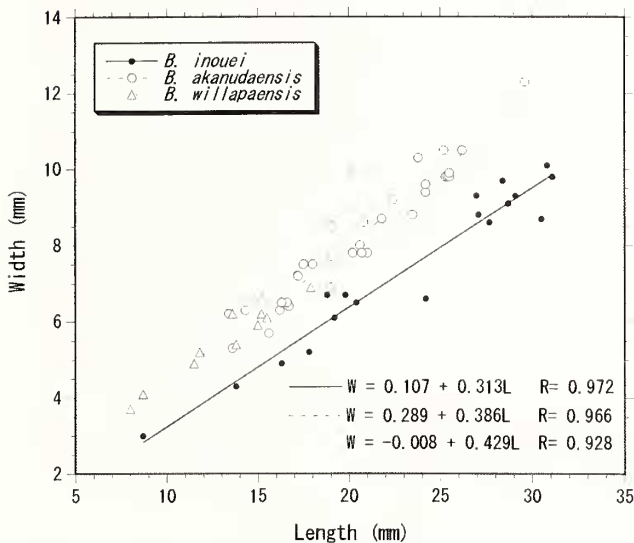


Figure 17. Ontogenetic changes in shell length and width of *Bathymodiolus* (sensu lato) *inouei*, *B.* (sensu lato) *willapaensis* and *B.* (sensu lato) *akanudaensis*.

Katto and Masuda (1978) as *Modiolus* sp. from the Oligocene? Muro Group in Wakayama Prefecture may be inferred as *Bathymodiolus* (sensu lato) by the occurrence from the carbonate in association with chemosynthetic species. This specimen is similar to the new species in its shell outline. However, owing to a few data on its specimen, it is necessary to collect additional specimens for comparing with this new species in detail.

Distribution: Known only from type locality. Lower Oligocene Nuibetsu Formation in Hokkaido.

Etymology: Named after Mr. Kiyokazu Inoue, Obihiro City, an amateur collector of molluscan fossils, who found the locality of this new species.

DISCUSSION

Only four Paleogene species of *Bathymodiolus* (sensu lato) are presently known. Among them, *B. willapaensis* is the oldest species, having been reported from middle Eocene to late Oligocene seep carbonates in Washington State, USA (Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Squires, 1993; Goedert and Campbell 1995; Kiel, 2006). Probably, the next oldest record is the present new species from the lower Oligocene. Kiel et al. (2010) described *B. palmarensis* from the “Oligocene” in Colombia, but its precise age is uncertain. Moreover, one specimen was illustrated as *Modiolus* sp. from the Oligocene? Muro Group in Wakayama Prefecture, central Honshu by Katto and Masuda (1978). All Paleogene species are small (less than 50 mm) and have their beak located near the anterior end which is one of the diagnostic features of *Bathymodiolus childressi* clade.

In contrast, many records of *Bathymodiolus* (sensu lato) are known from the Neogene deposits around the world. *Bathymodiolus akanudaensis* and *B.*? sp. occur in a middle Miocene deposit in central Honshu (Kuroda, 1931; Tanaka, 1959; Nobuhara et al., 2009; Amano et al., 2004, 2010). In the Caribbean area, two bathymodioline species have been described from the Miocene Freeman’s Bay Limestone of the late middle Miocene Lengua Formation in Trinidad and from the lower to middle Miocene Husto Clay Member of the Pozon Formation in Venezuela (Gill et al., 2005). *Modiolus* (*Modiolus*) *exbrochii exbrochii* Sacco and an elongate *Bathymodiolus*-like fossil were reported from the upper Miocene “Carcari a *Lucina*” at Montepetra, Italy (Moroni, 1965; Taviani, 1994, 2001). Recently, Saether et al. (2010) described *Bathymodiolus* (sensu lato) *heretaunga* and *Gigantidas coseli* as new species from the ?late early to the earliest late Miocene in the North Island of New Zealand. Of Pliocene age is “*Bathymodiolus*” sp. reported by Nobuhara (2003) from siltstone of the Tamari Formation in the forearc basin of Honshu.

Considering the geographic distribution of these records, we suggest that the worldwide spread of *Bathymodiolus* (sensu lato) might occur by the late Miocene (Figure 18). This trend of geographic spread is the same to that of the large vesicomyids which is another characteristic taxa of chemosynthetic fauna (Taviani, 2001; Gill et al., 2005; Lucentte and Taviani, 2005; Amano and Kiel, 2007; Amano and Kiel, in press; Kiel and Peckmann, 2007; Campbell et al., 2008; Kiel and Amano, 2010). Moreover, this pattern is consistent with the molecular study of Miyazaki et al. (2008), who estimated that the worldwide spread of *Bathymodiolus* (sensu lato) took place during the middle Miocene.

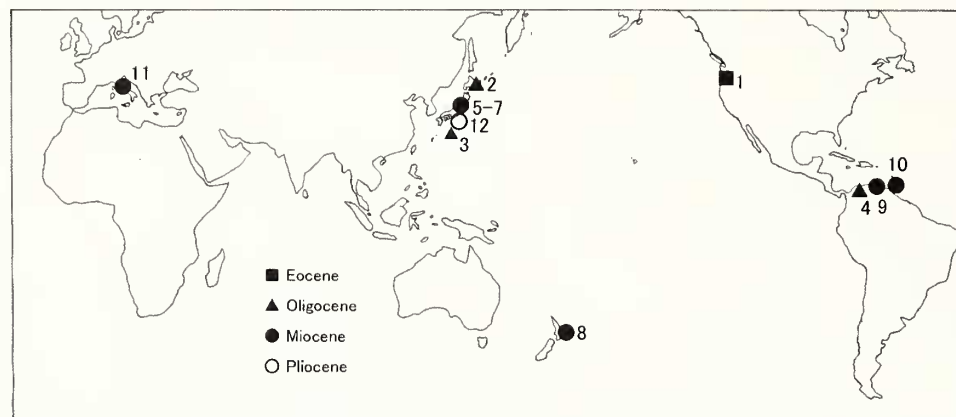


Figure 18. Distribution of the fossil *Bathymodiolus* (sensu lato). 1. *B. willapaensis* (Goedert and Squires, 1990; Squires and Goedert, 1991; Goedert and Squires 1993; Goedert and Campbell 1995; Kiel, 2006); 2. *B. inouei* (this study); 3. *Modiolus* sp. (Katto and Masuda, 1978); 4. *B. palmarensis* (Kiel et al., 2010); 5. *B. akanudaensis* (Kuroda, 1931; Tanaka, 1959; Nobuhara et al., 2009); 6. *B. akanudaensis* (Amano et al., 2010); 7. *B.*? sp. (Amano et al., 2004); 8. *Bathymodiolus* (sensu lato) *heretaunga* and *Gigantidas coseli* (Saether et al., 2010); 9. Venezuela bathymodioline (Gill et al., 2005); 10. Trinidad bathymodioline (Gill et al., 2005); 11. *Modiolus* (*Modiolus*) *exbrochii exbrochii* Sacco (Moroni, 1965; Taviani, 1994, 2001); 12. “*Bathymodiolus*” sp. (Nobuhara, 2003).

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